J. Malac. Soc. Aust. 4(3): 113-120. 30 June 1979.

STUDIES ON THE REPRODUCTIVE BIOLOGY OF GASTROPODS: PART 1. THE SYSTEMATIC DISTRIBUTION OF EGG RETENTION IN THE SUBCLASS PULMONATA (GASTROPODA)

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SUMMARY

Thus far, no pulmonate snail has been unequivocally demonstrated to be viviparous. Most pulmonate snails are oviparous, *i.e.* they release each egg immediately after its formation. On the basis of several years of observations and literature search, a list of known ovoviviparous pulmonates (here defined *sensu lato*, as those animals which retain their eggs instead of releasing them right away) is presented. Ovoviviparity is apparently rare compared with oviparity; it is absent from the entire freshwater order Basommatophora and from all families of slugs. Ovoviviparous reproduction is most common in such families as the Achatinidae, Subulinidae, as well as in several groups of the suborder Orthurethra. On the basis of this survey, it appears that while approximately one-half of the more than sixty families of stylommatophoran families contain at least one ovoviviparous species, the total number of species involved is small.

INTRODUCTION

Reproduction in pulmonate snails – as in other organisms – can be classified into three broad categories: oviparity, viviparity and ovoviviparity. The first term refers to parental organisms which deposit their eggs as soon as they are formed. In the second group, embryos are retained inside the parental organism, which supplies them with nourishment continuously during development. The third group of organisms, called ovoviviparous, retain the eggs inside part of the reproductive tract for some period of time, with the eggs usually hatching inside the parental body, but without having received nourishment other than what was initially contained inside the egg. Among land snails, there are a number of groups such as many Partulidae and Achatinidae which allow the young to hatch inside or carry (retain) the eggs for variable periods of time only to release eggs later, containing advanced embryos. Because of the widespread occurrence of irregularity in the duration of egg retention, the term ovoviviparity is used here to include all those snails which retain eggs from a few days to several weeks, though they eventually hatch either inside the parental body or outside of it. The term "egg retention" may be substituted here for "ovoviviparity".

All animals which are ovoviviparous *sensu strictu* (young hatching from the egg while inside the parent) are egg retainers, but not all egg retainers are ovoviviparous in the strictest sense of the word, only *sensu lato*, as used in this paper. Such a general definition is necessary for the practical consideration of reproductive strategies in land snails and is discussed in greater detail elsewhere (Tompa, in preparation).

The approach for this study was to search for living and preserved specimens containing eggs with advanced embryos. Oviparous snails lay eggs which have not yet undergone even first cleavage (Tompa, personal observations), whereas most ovoviviparous snails will be found to have gastrula and post-gastrula embryos inside their eggs. Therefore, only an ovoviviparous or egg retaining animal will ever be found to contain eggs with advanced young. It is because ovoviviparous animals carry their eggs for many days or weeks that they are often found in the gravid condition. On the other hand, such oviparous snails as *Anguispira, Helix, Polygyra* and even *Strophocheilus oblongus* with its giant eggs, form each egg within the space of 2-3 hours and lay them at intervals ranging from 15 minutes to 3 hours (unpublished). Since the total duration of egg formation and subsequent deposition in oviparous animals typically takes far less than a single day, these animals will be found in a gravid state only most rarely.

An examination of several thousand preserved museum specimens and field collected animals brought back to the laboratory during the past five years resulted in not a single strictly oviparous snail having been found gravid with eggs, while a high percentage of such ovoviviparous species as *Subulina, Achatina* or *Partula* are gravid during the warm seasons. It should be emphasized that ovoviviparous animals often contain not eggs, but young snails which have hatched from eggs while inside the parental uterus. Because these neonates make a first meal of their egg shell remnants immediately after hatching and therefore leave no trace of them in the uterus, animals containing young were often automatically called viviparous in the early literature. However, the definition of viviparity is the provision of continuous nourishment/waste removal to the embryo through some morphological connection, and not a single species of pulmonate snail has been shown to satisfy this criterion. Thus, while by far the largest group of pulmonates are strictly oviparous and a few are ovoviviparous, none can be called viviparous at this time.

The present paper is an attempt to be as comprehensive as possible in listing the rather few cases of demonstrated ovoviviparity (egg retention). The older literature was searched, original descriptions were read and evaluated for accuracy, and the nomenclature was updated (originally almost all land snails were in the genus *Helix*). The only previous attempt at such a compilation was by Pelseneer (1935), but this list is incomplete and the names and systematic positions of the groups as originally presented are now out of date. Originally, I prepared this list for my own use during studies of the evolution of reproduction in gastropods; I present it here in the hope that other malacologists also need such information and will find this a newer starting point for research.

This list is surely not final, but I think one point does emerge clearly, that among pulmonate groups the occurrence of ovoviviparity is irregular and that conspicuously absent from this list are all of the Basommatophora and the various slug families. A similar compilation of reproductive patterns for the remaining Euthyneura and for the Prosobranchia, with an examination of egg morphologies, is in preparation. A

previous paper, which lists the distribution, mineralogy and ultrastructure of stylommatophoran eggs having a calcium carbonate shell, may provide some supplementary information (Tompa, 1976, *J. Morphology 150;* 861-888).

SYSTEMATIC DISTRIBUTION

	Source
CLASS GASTROPODA	
Subclass Pulmonata	
Order Basommatophora – no ovoviviparous (or viviparous species known)	Tompa
Order Stylommatophora	
Suborder Orthurethra	
ACHATINELLIDAE	
Subfamily Pitysinae	
Celticola	Cooke & Kondo (1960)
Tubuaia	"
Subfamily Lamellideinae	
Lamellidea	"
Tornatellinops	"
Subfamily Tornatellininae	
Elasmias	"
Fernandezia	"
Tornatellina	"
Subfamily Tornatellidinae	
Philopoa	"
Tornatellides	"
Subfamily Achatinellinae	
Achatinella	"
Newcombia	"
Partulina	"
Perdicella	"
Subfamily Tekoulininae	
Tekoulina pricei	Solem (1972)
[a] PARTULIDAE	
Eua sp.	Tompa
Partula spp.	Tompa
Samoana spp.	Tompa
[b] AMASTRIDAE	
Subfamily Amastrinae	Thiele (1935); Zilch (1959-60)
PYRAMIDULIDAE	
Pyramidula rupestris	Bronn (1912-28); Germain (1930); Taylor (1914); Collier (1889); Tryon & Pilsbry (1885-1937)
VALLONIIDAE	
Pupisoma	Thiele (1935); Gude (1914); Pilsbry (1948)

a) This whole family may be entirely ovoviviparous.
b) The other subfamily, Leptachatininae, is entirely oviparous.

Zoogenetes (Acanthinula) harpa	Steenberg (1925); Pelseneer (1935); Thiele (1935); Tryon & Pilsbry (1885-1937)
PLEURODISCIDAE	Thiele (1935)
Pleurodiscus balmei	Watson (1920); Tryon & Pilsbry (1885-1937)
PUPILLIDAE	
Lauria cylindracea	Steenberg (1925); Zilch (1959-60); Germain (1930); Grasse (1968)
Pupilla cupa	Steenberg (1925)
Pupilla muscorum	Tompa
Pupilla triplicata	Steenberg (1925)
VERTIGINIDAE[c]	Tryon & Pilsbry (1885-1937)
Subfamily Truncatellininae	
Bothriopupa tenvidens	"
Pronesopupa (Edentulopupa) admosta	"
Subfamily Nesopupinae – (ovoviviparity may be universal)	"
Lyropupa (Mirapupa) perlonga	"
Nesopupa (Nesopupilla) plicifera	"
Nesopupa (Limbatipupa) newcombi	"
ENIDAE	
Rachis (Buliminus) burnayi	Pelseneer (1935)
Suborder Mesurethra	
CLAUSILIIDAE	
Balea perversa	Pelseneer (1935); Watson (1920); Craven & Smith (1891); Germain (1930)
Clausilia conchinchinensi	Pelseneer (1935)
C. similis	Pelseneer (1935)
C. (Iphigena) ventricosa	Pelseneer (1935); Germain (1930); Loosjes (1941)
Euphaedusa tetsui	Loosjes (1941)
Laciniaria (Alinda) biplicata	Germain (1930); Loosjes (1941)
L. strauchi	Lezhava (1962)
Vestia turgida	Husana (1965)
CORILLIDAE	
Corilla	Thiele (1935); Gude (1914)
C. erronea	Pelseneer (1935)
Plectopylis	Thiele (1935); Gude (1914); Tryon & Pilsbry (1885-1937)
Suborder Sigmurethra	
FERRUSSACIIDAE	
Caecilioides acicula	Wachtler (1929)
C. consobrina	Tompa
C. gundlachi	Tompa

c) Likehachev and Rammelmeier consider the Vertiginidae to be a family of the Pupillidae; they call the former group viviparous. Grasse calls the family Vertiginidae generally oviparous.

Ferrussacia follicula	Pelseneer (1935); Germain (1930); Watson (1928)
F. (Glandina) lamellifera	Pelseneer (1935)
F. oranensis	Pelseneer (1935); Watson (1928)
F. (Glandina) procerula	Pelseneer (1935)
STREPTAXIDAE	
Ennea	Gude (1914)
Streptaxis burmanius	Pelseneer (1935)
Streptaxis obtusus	Pelseneer (1935)
Streptostele crassicostata	Pelseneer (1935)
S. crassicrenulata	Tompa
S. horei	Venmans (1955)
SPIRAXIDAE	
Spiraxis terebella	Tompa
[d] ACHATINIDAE	
Achatina alabaster	Pelseneer (1935)
A. crawfordi	Pelseneer (1935); Clapp (1897)
A. erronea	Pelseneer (1935)
A. flammea	Pelseneer (1935)
A. panthera	Pelseneer (1935)
A. zebra	Pelseneer (1935)
Burtoa nilotica	Reynell (1906); (but see Owiny, 1974)
Cochlitoma	Standen (1917)
Liguus	Standen (1917)
Limicolaria martensiana	Owiny (1974)
L. smithi	Robson (1912)
[d] SUBULINIDAE	
Glessula	Standen (1917)
Homorus mambocansi	Pelseneer (1935)
Leptinaria spp.	Pelseneer (1935)
Neoglessula vivipar	Zilch (1959-60)
Obeliscus	Zilch (1959-60)
Obeliscus obeliscus	Spence (1919)
Opeas	Zilch (1959-60)
Opeas dominicensis	Pelseneer (1935)
Opeas viviparus	Pelseneer (1935)
Pseudoglessula libera	Solem & van Bruggen (1976)
Rhodea	Zilch (1959-60)
Rumina decollata	Pelseneer (1935)
Stenogyra spp.	Pelsen eer (1935)
Subulina kassaiana	Venmans & Fromming (1957)
S. octona	Owiny (1974)
Zootecus	Zilch (1959-60)
RHYTIDIDAE (PARYPHANTIDAE)	
Delos (Rhenea) coresia	Kondo (1943)
Delos (Rhenea) voganus	Pelseneer (1935)
Ouagapia	Zilch (1959-60)
Ouagapia gradata	Kondo (1943)

d) Ovoviviparity is most common in this family and may be viewed as the dominant type of reproduction.

Ouagapia oualanensis	Kondo (1943)
Ouagapia rapida	Kondo (1943)
Ouagapia ratusukuni	Kondo (1943)
Priodiscus	Thiele (1935)
Rhytida aequalis	Pelseneer (1935)
R. (Ptychorhytida) inaequalis	Kondo (1943); Pelseneer (1935)
ACAVIDAE	
Stylodon sp.	Zilch (1959-60); Tryon & Pilsbry (1885-1937)
Stylodon studeriana	Bronn (1912-28)
Stylodon unidentata	Bronn (1912-28)
HAPLOTREMATIDAE	Thiele (1935)
Haplotrema (Anisotrema) sportella	Baker (1930)
[e] *Zophos voganus*	Pelseneer (1935)
UROCOPTIDAE	
Apoma	Zilch (1959-60)
Brachypodella agnesiana	Spence (1916)
B. chemnitzia	Spence (1916)
B. gracilis	Spence (1916)
B. obesa	Spence (1916); Clapp (1915)
B. suturalis	Spence (1916); Clapp (1915)
ENDODONTIDAE	
[f g] *Helicodiscus parallelus*	Tompa; Gugler (1972)
VITRINIDAE	
[h] *Vitrina* sp.	Pelseneer (1935)
EUCONULIDAE	
Guppya gundlachi	Baker (1925)
Guppya (Conulus) vacans	Pelseneer (1935)
Lamprocystis	Thiele (1935)
Microcystis myops	Pelseneer (1935); Grassé (1968) (subfamily ovoviviparous)
Sitalina	Thiele (1935)
[j] ARIOPHANTIDAE	
Louisia	Thiele (1935)
Pachystyla inversicolor	Pelseneer (1935)

e) Grassé calls this a streptaxid of the subfamily Zophinae; I have followed Zilch's assignment by placing it in the Haplotrematidae merely for convenience, as I am not familiar with this group's affinities.

f) Some place this genus in its own family, the Helicodiscidae; I have again followed Zilch for the convenience of keeping everything according to one system, unless obviously incorrect. This genus, *Helicodiscus*, appears to be a closely related group, entirely ovoviviparous.

g) The endodontid *Anguispira kochi*, reported to be viviparous by Gugler (C. Gugler, 1973, Amer. Malac. Un. Bull. 38; 10) is definitely oviparous. I have personally examined this snail and have bred it in my laboratory. No doubt, what Gugler examined was an *Oreohelix*.

h) This record is questionable and because of its singular report from an entire family it ought to be re-examined before being accepted with certainty. Nevertheless, I include it in this list to call it to attention.

j) The affinities of these genera are not clear to me; Zilch includes them in the family Ariophantidae whereas Thiele calls them members of the Helicarionidae.

SYSTROPHIIDAE (SCOLODONTIDAE)	
Miradiscops variolata	Baker (1925)
Scolodonta cayennensis	Baker (1925)
S. eudiscus	Tompa
S. thomasi	Tompa
Tamayoa trinitaria	Baker (1925)
SAGDIDAE	
Hojeda	Thiele (1935)
H. peraffinis	Tryon & Pilsbry (1885-1937)
H. vortex	Tryon & Pilsbry (1885-1937)
Sagda haldeniana	Pelseneer (1935)
Zaphysema	Pelseneer (1935)
Z. tenerrima	Tryon & Pilsbry (1885-1937)
OREOHELICIDAE	
k *Oreohelix*	Pilsbry (1948)
O. strigosa	Bavay (1884)
O. vortex	Solem (1975)
O. waltoni	Solem (1975)
Radiocentrum	Zilch (1959-60)
BRADYBAENIDAE	
h *Euhadra luchuana*	Pelseneer (1935)
HELICIDAE	
h *Theba cartusiana*	Hopwood (1944)
UROCYCLIDAE	
Trochozonites ibuensis	Lamy (1929)

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k) Zilch is incorrect in considering the subgenus *Oreohelix* to be oviparous and the other related subgenus of *Oreohelix (sensu latu)*. *Radiocentrum*. to be ovoviviparous; the facts are *vice versa*.

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